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A LITERARY NOTE ON THE LAW OF GERMINAL CONTINUITY

The distinctive theory of germinal continuity or continuity of the germ-plasm is, historically speaking, of much more recent origin that the broader doctrine of genetic continuity from which it was derived and with which, in the usage of some writers, it is made synonymous. Genetic continuity in its widest sense embodies the proposition that "living matter always arises by the agency of preexisting living matter,"[1] and in a more restricted sense means that all living cells must be derived by continuous lineage from the cells of preexisting generations. The theory of germinal continuity, in its most highly developed form, conceives the germinal protoplasm as dividing into two portions, from one of which the somatic or body cells of the offspring are developed while the other portion is reserved unchanged for the formation of the reproductive material of the adult individual. The general doctrine of continuity is fundamentally essential to both these theories, but germinal continuity, at least in any Weismannian sense, always involves the further assumption of a transmission from generation to generation of an unmodified residue of the specially organized germinal substance, the germ-plasm, through a definite series of cells, but this concept does not imply that there is necessarily a direct connection between the germ-cells of consecutive generations.

To Richard Owen the credit is usually given of being the first to recognize the distinction between body-cells and germ-cells and thus to foreshadow the idea of germinal continuity. Writing in 1849, he said:

> Not all the progeny of the primary impregnated germ-cell are required for the formation of the body in all animals: certain of the derivative germ-cells may remain unchanged and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell or the nucleus of such may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual; and this may be, or

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[1] Huxley, T. H., "Lay Sermons, Addresses and Reviews," New York, 1870, p. 350.

> may not be, like that individual in which the secondary germ-cell or germ-mass was included.
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> When the primary division of the impregnated germ-cell takes place, it must divide its properties with its matter between the two cells resulting from the spontaneous fission of its nucleus: and this result must follow every subsequent division. It is scarcely figurative therefore to say that the primary or parent germ-cell has equally divided its spermatic virtue amongst its countless progeny.[2]

Owen's suggestions apparently received no consideration and were later disregarded by the author himself. Somewhat similar ideas were expressed by Haeckel[3] in some of his earlier speculations. Galton, says Weismann,[4] was the first to express ideas resembling the theory of germinal continuity, but these ideas were later considerably modified.[5]

A clear expression of the conception of germinal continuity is found in the writings of Jäger, but his ideas made little impression, and inaccurate citation of his work has sometimes caused his disparagement. In 1877, restating previously expressed propositions, he said:[6]

> The basis of heredity consists in this, that throughout whole series of generations the germ-protoplasm of animals retains unchanged its specific quality in spite of all external influences. In the actual ontogeny the available germ-protoplasm may divide into two groups, the *ontogenetic,* from which the existing individual is formed, and the *phylo-*

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[2] Owen, Richard, "On Parthenogenesis," London, 1849, pp. 5–6, 63–64.

[3] Haeckel, E., "Generelle Morphologie," 1866, pp. 287–289.

[4] Weismann, A., "The Germ-plasm, A Theory of Heredity," New York, 1902, p. 198.

[5] Galton's early ideas were expressed as follows:

"From the well-known circumstance that an individual may transmit to his descendants ancestral qualities which he does not himself possess, we are assured that they could not have been altogether destroyed in him, but must have maintained their existence in a latent form. Therefore each individual may properly be conceived as consisting of two parts, one of which is latent and only known to us by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses.

"The adjacent and, in a broad sense, separate lines of growth in which the patent and latent elements are situated, diverge from a common group and converge to a common contribution, because they were both evolved out of elements contained in a structureless ovum, and they, jointly, contribute the elements which form the structureless ova of their offspring."—Galton, F., "On Blood-relationship," *Proceedings of the Royal Society of London,* Vol. 20, 1872, p. 394.

[6] Jäger, G., "Physiologische Briefe," *Kosmos,* Jahrg. I, Bd. I, 1877, p. 17.

genetic, which is reserved until the time of puberty for the formation of the reproductive material. This reservation of the phylogenetic material I designated as the Continuity of the Germ-protoplasm.[7]

This clear expression of the doctrine of germinal continuity apparently does not appear in Jäger's later work,[8] to which reference is usually made.

Weismann in his essay on the "Continuity of the Germ-plasm,"[9] assumed that he was the first to give expression to this conception but in a later work[10] made acknowledgments to other authors who had anticipated his theory. With respect to Jäger, however, he said:[11]

> The praiseworthy attempt to do justice to my predecessors in this particular subject has perhaps been carried too far. In Geddes and Thompson's "Evolution of Sex" (p. 93), for instance, a quotation is given from Jäger which seems to prove that he anticipated me with regard to the theory under consideration. The quotation in which this idea is expressed is, however, not taken from the book published in 1878 but from an essay written ten years later, and it concludes with the following words: "This reservation of the phylogenetic material I described as *the continuity of the germ-plasm.*" But no mention is made by Jäger of the continuity of the germ-plasm in his book which ap-

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[7] The original language of these statements is as follows: "In der 'Zeitschrift für wissenschaftliche Zoologie' Bd. XXVII habe ich unter den Titel 'Ueber die Bedeutung der Geschmak- und Geruchstoffe' ein Erörterung der chemischen Seite der Vererbungsfrage gegeben, nachdem ich schon vorher in meinen 'Zoologischen Briefen' der physikalischen Seite einige Betrachtungen gewidmet hatte. Ich will es um Folgenden versuchen, dieser Frage einige neue Anhaltspunkte abzugewinnen und das dort Gesagte zu ergänzen.

"Meine früheren Auseinandersetzungen gingen dahin: Das Fundament der Vererbung besteht darin, dass durch grosse Reihen von Generationen hindurch das Keim Protoplasma eines Thieres eine sich stets gleichbleibende spezifische Beschaffenheit allen Anfechtungen von aussen zum Trotz bewahre. Ich sagte: Bei der jedesmaligen Ontogenese scheide sich das verfügbare Keimprotoplasma in zwei Gruppen, die *ontogenetische,* aus welcher das jeweilige Individuum aufgebaut wird und die *phylogenetische* welche reservirt werde, um zur Zeit der Geschlechtsreife die Fortpflanzungstoffe zu bilden. Diese Reservirung des phylogenetischen Materials bezeichnete ich als Continuität des Keimprotoplasmas."

[8] Jäger, G., "Lehrbuch der allgemeinen Zoologie," Leipzig, 1878, II Abtheilung.

[9] "Der Continuität des Keimplasmas," Jena, 1885; Essay IV in authorized translation, 2d ed., 1891, p. 163.

[10] "The Germ-Plasm, A Theory of Heredity," New York, 1902, pp. 198–202.

[11] *L. c.,* p. 200, footnote.

peared in 1878, in which a connection between the germ-*cells* of different generations is supposed to exist:—and this is not the case. The entirely new statement of his ideas has been influenced by those contained in my essays which had appeared in the meanwhile.

As a matter of fact the quotation from Jäger which Weismann repudiates actually appeared more than eight years before the publication of Weismann's essays, as the quotation from *Kosmos,* given above, clearly shows. Although Jäger coined the expression "Continuity of the Germ-plasm," the idea involved seems to have attracted no attention until after the essays of Weismann had aroused general scientific interest.

Jäger also assumed a material connection between the germ-*cells* of different generations,[12] and, in what Weismann characterizes as "a few casual remarks," Rauber[13] expressed a conception which some authors interpret as the same idea.

In the account of his exhaustive researches on the differentiation of the reproductive cells Nussbaum gave clear expression to the doctrine of the continuity of the germ-*cells,* which in a strict sense means that germ-cells arise directly from one another. The views held by Nussbaum[14] were in part set forth in the following words:

[12] See preceding quotations from Weismann.

[13] Rauber, A., "Formbildung und Formstörung in der Entwicklung von Wirbelthieren," *Morphologische Jahrbuch,* Vol. 6, 1880, p. 4. The "casual remarks" are as follows:

"Die beiden Theilstücke, deren Verbindung das neue Wesen bewirkt, sind bei den höheren Thierformen enthalten in besonderen Organen, den Keimdrüsen. Da aber die Keimdrüsen die folgende Generation beherbergen, so erscheint ein Individuum als der Träger zweier Generationen, seiner eigenen sowie der folgenden Generation. Insoweit er der Träger seiner selbst ist, stellt er eine Person im engeren Sinne dar; er ist der *Personaltheil* der dualistischen Anlage. Die Träger der Zukünftigen Generation, die Keimdrüsen, stellen dagegen den *Germinaltheil* der dualistischen Anlage dar.

"Personal- und Germinaltheil gehen aber von *einem* befruchteten Ei aus, *ein* solches Ei enthält den Stoff mit dem Kräfteplan zu der genannten dualistischen Anlage. Man kann darum auch von einem Personaltheil und Germinaltheil des befruchteten Eies reden."

[14] Nussbaum, M., "Zur Differenzierung des Geschlechts im Thierreich," *Archiv für mikroskopische Anatomie,* Bd. 18, 1880, p. 112. The text of the original is worded thus:

"Es theilt sich demgemäss das gefurchte Ei in das Zellenmaterial des Individuums und in die Zellen für die Erhaltung der Art. In beiden Theilen geht die Zellenvermehrung continuirlich weiter; nur tritt im Leibe des Individuums die Arbeitstheilung hinzu, während in seinen Geschlechtszellen sich eine einfache additionelle Theilung vollzieht. Die beiden Zellen-

> The segmented ovum divides into the cell-material of the individual and into the cells for the preservation of the species. In both divisions the cell-multiplication proceeds continuously, but in the body of the individual division of labor occurs, while in the reproductive cells simple division only takes place. Both groups of cells and their offspring are propagated quite independently of each other, so that the reproductive cells have no share in the development of the tissues of the individual, and no seminal or ovicular cell arises from the cell-material of the individual. After the segregation of the reproductive cells the history of the individual and that of the species are entirely distinct, and because of this relation the "constancy" of the species is more easily understood; that is, the sharp persistence of the phenomenon of atavism by means of which ancestral traits are transmitted. For sperm and ovum are not derived from the cell-material of the parent organism, but have a common origin with it. However, since they are preserved within it, they are subject to the conditions which modify the parent organism; therefore the transmission of "acquired" characteristics is not excluded.

Nussbaum is said by some to be the first to suggest the idea of the cellular continuity of successive generations, but this conception is clearly implied in Virchow's aphorism[15] ''omnis cellula a cellula,'' and was fully stated in 1858 in the Law of Genetic Cellular Continuity first clearly formulated by Virchow[16] as follows:

> Just as an animal can originate only from an animal and a plant only from a plant, so every cell must arise from a preexisting cell. Although there are individual cases in which strict proof is still wanting, yet the principle is firmly established that for all living beings, whether they be entire plants or animal organisms or integrant parts of the same, there exists an eternal law of *continuous development.*

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gruppen und ihre Abkömmlinge vermehren sich aber durchaus unabhängig von einander, so dass die Geschlechtszellen an dem Aufbau der Gewebe des Individuums keinen Antheil haben, und aus dem Zellenmaterial des Individuums keine einzige Samen- oder Eizelle hervorgeht. Nach der Abspaltung der Geschlechtszellen sind die Conti des Individuums und der Art völlig getrennt, und wir glauben aus diesem Verhalten die 'Constanz' der Art, d.h. die in der Erscheinung des Atavismus gipfelnde Zähigkeit, mit der sich die Eigenthümlichkeiten der Vorfahren vererben, begreiflicher zu finden. Denn Samen und Ei stammen nicht von dem Zellenmaterial des elterlichen Organismus ab, sondern haben mit ihm gleichen Ursprung; da sie aber in ihm aufbewahrt werden, so sind sie auch den Bedingungen unterworfen, welche auf den elterlichen Organismus modificirend einwirken, weshalb die Vererbung der 'erworbenen' Eigenschaften nicht ausgeschlossen ist.''

[15] *Archiv für Pathologische Anatomie,* Bd. 8, 1855, p. 23.

[16] ''Die Cellularpathologie im ihrer Begründung auf physiologische und pathologische Gewebelehre,'' Berlin, 1858, p. 25.

On the other hand, to Nussbaum is sometimes credited the theory of germinal continuity, but in such cases authors apparently do not sharply distinguish continuity of the germ-*plasm* from continuity of the germ-*cells*. Thus Minot[17] says:

> We owe to Moritz Nussbaum the theory of germinal continuity—the only theory of heredity which seems tenable at the present time. According to this theory, the germ-cells are set aside during the segmentation of the ovum and preserve the essentially undifferentiated qualities of the protoplasm and nucleus of the ovum, from the division of which they arise.

However, irrespective of the conclusions that may be reached as to whom priority in the statement of the theory of germinal continuity belongs, it is to Weismann that credit must be given for the development of this doctrine into an important theory of heredity.

There would seem to be a gain in precision and clearness of expression in discussions involving the idea of continuity in development if a distinction were always made between (1) *genetic continuity, or biogenesis,* (2) *genetic cellular continuity,* (3) *continuity of the germ-cell* and (4) *germinal continuity.* Thus restricted the term germinal continuity expresses more closely the conception held by the greatest exponent of this theory. Since Jäger first used the phrase "Continuity of the Germ-plasm" I suggest that his name be linked with that of Weismann in referring to this principle, which may well be called the Jäger-Weismann Law of Germinal Continuity, the esential doctrine of which is thus expressed:[18]

> In each ontogeny, a part of the specific germ-plasm contained in the parent egg-cell is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation.

However, the real significance of Weismann's theory of germinal continuity and its bearing on theories of heredity can not be fully appreciated without at least a general acquaintance with the somewhat voluminous literature of this subject.

W. W. STOCKBERGER

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[17] Minot, C. S., "Laboratory Text Book of Embryology," Philadelphia, 1910, p. 28.

[18] Weismann, A., "Essays upon Heredity and Kindred Biological Problems," authorized translation, 2d edition, Oxford, 1891, p. 170.